

AN AGENT-BASED MODEL OF WILDLIFE MIGRATORY PATTERNS IN
HUMAN-DISTURBED LANDSCAPES

by

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THESIS ABSTRACT

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In recent years, human decision-making has led to significant landscape impacts in the western United States. Specifically, migratory wildlife populations have increasingly been impacted by rural urban development and energy resource development. This research presents the application of agent-based modeling to explore how such impacts influence the characteristics of migratory animal movement, focusing on mule deer (*Odocoileus hemionus*) in Western Wyoming. This study utilizes complex adaptive systems and agent-based modeling frameworks to increase understanding of migratory patterns in a changing landscape and explores thresholds of interference to migration patterns due to increased habitat degradation and fragmentation. The agent-based model utilizes GPS-collar data to examine how individual processes lead to population-level patterns of movement and adaptation. The assessment incorporates elements from both human and natural systems to explore potential future scenarios for human development in the natural landscape and incorporates adaptive behaviors, as well as animal-movement ecology, in changing landscapes.

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CHAPTER I

INTRODUCTION

In recent years, mule deer (*Odocoileus hemionus*) in Wyoming and across much of the western United States have received a great deal of attention in academic, management, and public spheres (Gorman, 2015; Ostlind and Riis, 2014; Howard, 2014). Mule deer populations have declined in western Wyoming in recent decades, due in part to habitat loss from anthropogenic landscape change (Polfus, 2011). One driver of landscape change in this area has been increased oil, coal, natural gas, and energy resource development in the last few decades, particularly in response to concerns regarding national energy needs and national security (Hebblewhite, 2011). Wyoming is among the highest energy producing states in the United States, leading the nation in coal production, and is one of the top natural gas producers, with 22,171 active natural gas wells (EIA, 2014). Much of this energy production overlaps with critical mule deer, sage grouse (*Centrocercus urophasianus*), and pronghorn (*Antilocapra americana*) habitat (Sawyer et al., 2006; Holloran et al., 2010; Beckmann et al., 2012). These species spend winter months in a sagebrush steppe habitat, and such development can impact how animals utilize seasonal ranges (Sawyer et al., 2006; Beckmann et al., 2012), as well as the migratory patterns of animals such as mule deer that move through these development sites (Lendrum et al., 2012, 2013; Sawyer et al., 2013).

In addition to energy development, Wyoming's rising population has led to an increase in urban development that has impacted mule deer habitat. Between 2000 and 2010, the population of Wyoming increased by 13.1% (Polfus and Krausman, 2012). Urban development in the Rocky Mountain West (often characterized as rural residential

development) is continually expanding into ungulate habitats, which can lead to behavioral and demographical effects on these animals (Polfus and Krausman, 2012). The majority of private land where urban development occurs is in lower elevations (Knight et al., 1995; Gude et al., 2006) that often coincide with critical winter deer habitat (Safford, 2003). Urban and other types of development can lead to fragmentation of intact landscapes (Polfus, 2012), but there is limited understanding of how such fragmentation impacts ungulates at the population-level (Hebblewhite, 2011).

Understanding how energy and urban development impact mule deer populations requires a better understanding of how these forms of development impact their migratory patterns. Animal movement and migration have been the focus of much theoretical and empirical work in ecology over the last twenty-five years, primarily because the movement of individuals provides a spatio-temporal bridge between the individual and the population (Turchin, 1998; Schick et al., 2008). By studying individual movement, ecologists, wildlife biologists, and geographers are able to gain greater insight into spatial dynamics of migratory wildlife (Bowler and Benton, 2005; Schick et al., 2008). Spatial data collected from GPS collars provide new opportunities to explore how environment influences the movement behavior of animals (Schick et al., 2008).

Continued progress in movement behavior within ecology will require developing models for realistic movement behavior, inferring how the organism-environment interaction influences movement behavior, and inferring movement itself when movement data are incomplete or imprecise (Schick et al., 2008). Ecologists have focused on the interaction between individuals and their environment in an effort to understand future impacts from habitat change and loss (Schick et al., 2008). Past studies in animal movement have used

fractal analysis (Dicke & Burrough, 1988), first passage time (Fauchald & Tveraa, 2003), Lévy flights (Viswanathan et al., 1996), multi-behavioral analysis, hidden markov models (Blackwell, 2003), state-space models (Morales et al., 2004), and sophisticated hierarchical Bayesian models (Schick et al., 2008).

With methodological approaches to studying animal movement abound, attention to the impacts of development on mule deer populations requires further investigation. Prior research concerning the impacts of development on wildlife populations has focused largely on disturbances to animals residing in seasonal ranges (Dyer et al., 2002; Sawyer et al., 2006; Thomson et al., 2006), with less research exploring how energy and urban development potentially alter their migratory patterns (Polfus and Krausman, 2012). Several researchers have called for efforts to improve our understanding of the impacts of development on ungulate migratory patterns through modeling and mapping techniques that examine multiple barriers to migration in order to inform planners and decision-makers of potential impacts from different types of development scenarios (Copeland et al., 2009). Furthermore, empirical data and results from prior impact studies have aided in efforts of identifying migration corridors of concern for conservation (Sawyer et al., 2009), and there is a growing interest in how development, in the form of semi-permeable barriers, impacts migratory behavior (Sawyer et al., 2013). However, research has yet to emerge that investigates how future landscape changes from both urban and energy development together will potentially change fitness (condition) and migratory dynamics of mule deer. Further exploration of modeling approaches have the potential to provide new insight into the dynamic nature of mule deer migration in response to a development-driven, dynamic landscape.

A complex systems approach to understanding the impacts of development on mule deer migration is promising because it provides an opportunity to evaluate multiple stressors to mule deer, as well as examine impacts at a population-level. In recent years the application of complex systems modeling in understanding animal movement has provided a basis for further understanding the underlying processes that drive animal behavior and spatial decision-making (Tang and Bennett, 2010), with particular studies focusing on ungulates navigating changing landscapes (Bennett and Tang, 2006; Dyer et al., 2002; Semeniuk et al., 2012). The development of agent-based models to examine wildlife movement and behavior have expanded to include a variety of ungulate species, including elk (Bennett and Tang, 2006), caribou (Semeniuk et al., 2012), and moose (Grosman et al., 2011). Such work provides a basis for developing an agent-based model to assess impacts of development on mule deer and other wildlife navigating a changing landscape. Additionally, social scientists and ecologists can utilize agent-based models to further explore decision-making and interactions of individuals at various scales (Bousquet and Le Page, 2004). The incorporation of both adaptive behaviors and animal-movement ecology in a dynamic landscape with possible alternative futures is a mostly untapped potential of complex systems modeling (McLane et al., 2011). Improved understanding of animals' responses to development activities could help design development plans that maintain necessary wildlife behaviors, including migration (Lendrum et al., 2012).

The objective of this research is to use a complex systems modeling approach to evaluate: *how do the spatial arrangement and extent of urban and energy development impact migrating mule deer populations in Western Wyoming?* To answer this question,

this study examines the migratory patterns of mule deer in the Upper Green River Basin of Western Wyoming, USA through an agent-based modeling approach. This research integrates multiple stressors to migratory wildlife (both urban and energy development simultaneously), and allows for experimental study of pre and post development states. In developing a complex systems model for mule deer, findings from this research have the potential to aid multiple stakeholders in further understanding the potential impacts of urban and energy development on mule deer populations, and to expand prior and ongoing studies of migratory ungulates in the increasingly developed Western Wyoming landscape. Increased understanding of the impacts and thresholds has the potential to further research in mitigating impacts to wildlife in other regions from development activities, and also has the potential to increase stakeholder knowledge, leading to the development of informed policy and planning strategies for urban and energy development projects.

CHAPTER II

METHODS

Study Site and Data

The subpopulations for this study include mule deer that winter in the Mesa and Ryegrass-Soapholes study areas, both subpopulations of the larger Sublette Herd Unit (Copeland et al., 2014). Mule deer wintering in the Mesa and Ryegrass-Soapholes study areas migrate each spring to summer ranges and make their way back to winter ranges each fall (Sawyer et al., 2005) (see Figure 1). Vegetation, climate, elevation, and other environmental elements drive mule deer migrations, and human impacts and presence in the landscape can also influence movement behaviors (Monteith et al., 2011). Further expansion of urban and energy development could negatively impact these migratory deer populations.

Mule deer applied in this study are from the Mesa and Ryegrass-Soapholes subpopulations of the larger Sublette herd unit (Copeland et al., 2014). The baseline mule deer abundance for the Mesa subpopulation of mule deer is estimated at 2,856, which was derived from averaging the winters of 2004-05 (2,818) and 2005-06 (2,894) (Sawyer and Nielson, 2012). GPS collars are programmed to collect locations every 2 hours during non-summer months and every 5 hours during summer (June 15 – September 15) (Sawyer and Nielson, 2012).

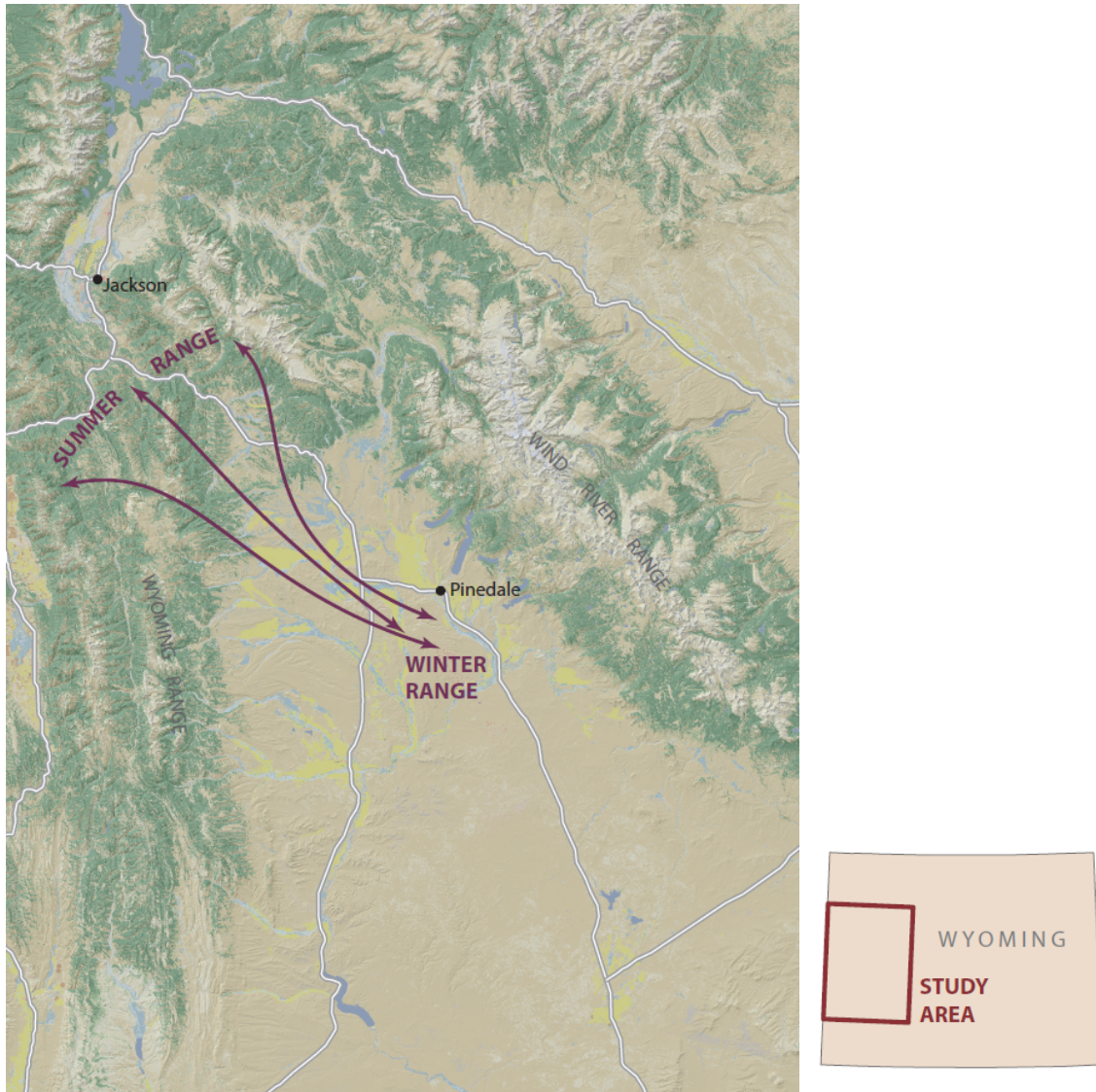


Figure 1: The study area, located in Western Wyoming just south of Yellowstone National Park, encompasses the entire Sublette Herd range. However, this study focuses solely on the Mesa and Ryegrass-Soapholes subpopulations.

This data was originally collected to monitor winter distribution as it relates to gas development and animal winter counts for mule deer in the Mesa and compare population changes with those observed in the larger Sublette herd unit (Sawyer and Nielson, 2012). However, the GPS data also provide an additional opportunity to delineate migration routes for these migratory populations (Sawyer and Nielson, 2012). Furthermore, this data provides an opportunity to utilize an agent-based modeling approach to explore impacts of development on mule deer, as well as develop ways in which collected GPS collar data can be applied to calibrate and validate these models.

Model Description

The model description follows the ODD (Overview, Design concepts, and Details) protocol (Grimm et al., 2010), which standardizes the process and descriptions of the components included in the agent-based model and aids in the ability to reproduce methods and analysis for future research. The model description begins with a general overview of model processes, and a more detailed explanation of model components follows.

1. Purpose

The purpose of this model is to assess the potential level of impact of urban and energy development to migratory wildlife populations. Specifically, this research aims to address the following question: *how do the spatial arrangement and extent of urban and energy development impact migrating mule deer populations in Western Wyoming?* This research expands upon previous research conducted by Sawyer et al. regarding impacts of

energy development on mule deer in Western Wyoming, and previous research on the impacts of urban and residential development (Polfus and Krausman, 2012). ‘Impacts’ to mule deer are defined in this study as changes in fitness and frequency of stress events due to changes in development expansion.

2. Entities, state variables, and scales

2.a. Agents/individuals

Mule deer are represented as mobile, migratory agents that make decisions based on internal and environmental states. There are a total of fifty-three mule deer agents in the model, a representative sample of the larger population. This value is derived from the total number of GPS collar datasets from 2010-2012 used for calibration and validation. Individuals have multiple internal states that allow them to make decisions to achieve their objective of maintaining sufficient fitness for survival and migrating between home ranges. Each agent has two home ranges assigned (summer and winter), based on a high fidelity (i.e. preference) that mule deer show to home ranges and migratory corridors (Brown, 1992; Garrott et al., 1987). Each deer also has a level of fitness that is an abstract representation of the health (or condition) of each deer. When fitness is above or below a set threshold, the deer will choose to continue migrating or to forage, respectively. If fitness falls below zero, the deer will transition to a stressed state. Each individual records its distance traveled, its fitness, and its frequency of stressed states. Based on internal states and external conditions, deer will make decisions to meet objectives of migration and maintaining sufficient fitness. All individuals represent adult, female deer, as only adult females were fitted with GPS collars, and the study does not include reproduction.

Reproduction was excluded from the model because this study begins in the fall and ends in the late-spring/early-summer before reproduction would occur.

2.b. Environment

The environment of the model consists of four input spatial datasets that define landscape variables. The spatial resolution of the input data is 200 m, and the entire extent of the study area is 160,000 m by 191,200 m. The temporal resolution of the model is two hours, and each simulation is performed for a total of 4380 time steps, representing a total time period of 365 days. The four input datasets include 1) mule deer home ranges, 2) 10 km buffer derived from GPS collar datasets, 3) landcover type, and 4) areas for development potential. The resolution of the inputs was determined by the processing ability of the modeling platform, and one dataset was downsampled from its original resolution to meet these requirements (see Table 1).

Mule deer home ranges are defined by the Wyoming Game and Fish Department (WGFD, 2013), and represent regions of both winter and summer ranges for the study area. The 10 km buffer derived from observed GPS collar locations of deer defines the range in which winter and summer ranges are selected for this sub-population to prevent deer from selecting unrealistic home ranges outside of the known migratory region. Deer can move and make decisions outside of this buffer zone, but based on observed data their selected home ranges will fall within the 10km buffer. Landcover type is defined by the National Landcover Dataset (NLCD, 2011), and provides landscape information of where vegetation is available for deer to forage and where development currently exists. The fourth input dataset defines areas with potential for development in the landscape. Potential development falls into two categories: urban and energy. This input defines the

bounds for these two types of development, and was derived from the Protected Areas Database of the United States (PAD-US, 2014) and a spatial dataset defining areas for potential energy development from the Wyoming Geological Survey (WGS, 2012) for both oil and natural gas. The PAD-US data define areas that fall under public and private ownership. If land is public and there is potential for energy development, well pads will be dispersed in these regions. If land is classified as private, only urban development will occur in these regions. These two datasets were merged to define areas for urban and energy development potential, and protected areas where development is prohibited or would potentially be unlikely due to some level of protection status. See Table 2 and Figure 2 for a detailed summary of environment attributes.

Table 1: Description of environmental input datasets and resampled resolutions.

Input dataset	Original file type	Original resolution	Resampled resolution
Mule deer home ranges (WGFD 2013)	Vector (polygon)	N/A	200 m
10 km buffer (derived from GPS collar datasets) (Sawyer and Nielsen 2012)	Vector (point)	N/A	200 m
Landcover type (NLCD 2011)	Raster	30 m	200 m
Energy development potential (WGS 2012)	Vector	N/A	200 m
Urban development potential (PAD-US 2014)	Vector	N/A	200 m

Table 2: Description of environment input data attributes and purpose in the model.

Input dataset	Categories (model value)	Description
Mule deer home ranges (WGFD 2013)	Winter range (3) Summer range (2) Other (1)	Areas where deer have been observed to be present seasonally
10 km buffer (Sawyer and Nielsen 2012)	Within buffer (100) Outside of buffer (1)	A 10 km buffer analysis of GPS collar locations of deer (Sawyer and Nielsen 2012) to define areas in which it would be probable seasonal home ranges would be located
Landcover type (NLCD 2011)	Shrub/scrub (1) Evergreen forest (2) Herbaceous (3) Deciduous forest (4) Woody wetlands (5) Emergent herbaceous wetlands (6) Hay/pasture (7) Developed, open space (8) Mixed forest (9) Barren land (10) Developed, low intensity (11) Open water (12) Developed, medium intensity (13) Cultivated crops (14) Perennial snow/ice (15) Developed, high intensity (16)	Vegetation types listed in order of deer preference. Deer preference is based off of the percentage of GPS locations on particular landcover types (see Table 3)
Energy development potential (WGS 2012) and urban development potential (PAD-US 2014)	Non-private land (0) Private land (1) Energy development potential, non-private land (2) Energy development potential, private land (3)	Energy development occurs in areas of non-private land with energy development potential (2). Urban development occurs on private land and in areas with energy development potential and private land (1,3). No development occurs on non-private or protected land (0).

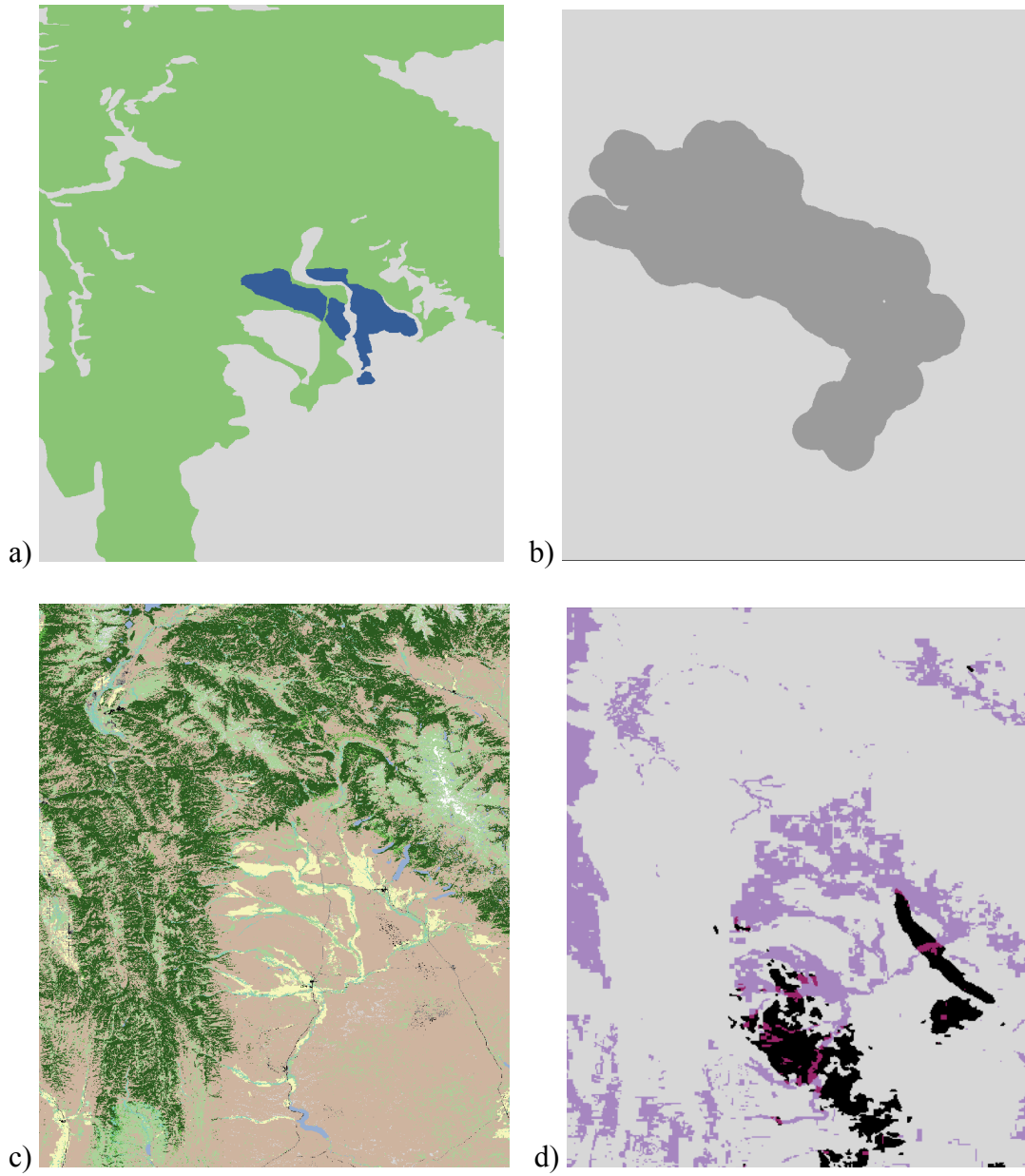


Figure 2: Environment input datasets for the model are: a) home ranges, including summer (green) and winter (blue), b) 10 km buffer surrounding GPS locations of mule deer, c) landcover type, and d) potential development areas, including energy (black) energy/urban (magenta), and urban (purple).

3. Process overview and scheduling

The model begins with setup of environmental variables, the initial locations of the deer, and the initial states of both deer and the environment. As a model simulation proceeds, urban development and energy development expand from existing development, and time progresses from fall to summer. In the fall, deer migrate from their summer range in higher elevations to their shared winter range in lower elevations, and in the spring, deer return to their summer ranges. The number of deer in the model remains constant at fifty-three (the number of GPS collar datasets applied in this study), and fitness for each deer is randomly selected. At each time step of the model deer make a decision to either stop and forage or continue to migrate. These decisions are based on internal states and the state of the immediate surrounding environment. If deer need to forage and there is sufficient or quality vegetation, they will stop and forage. If deer need to forage and there is not sufficient or quality vegetation they will continue to migrate until vegetation is available. Deer have a local knowledge of preferred vegetation type in their vicinity, as well as the presence of development barriers (i.e. urban or energy development in the landscape). Deer have a global knowledge of where their preferred summer and winter home ranges are located, and the direction in which they need to migrate to meet these objectives. This global knowledge is based on the strong fidelity that mule deer show to home ranges and migratory corridors (Brown, 1992; Garrott et al., 1987).

4. Design Concepts

4.a. Basic principles

All individuals in the model make decisions based on the same foraging and fitness rules. However, these rules lead to varied results for each individual based on landscape influences. Foraging and fitness principles were derived from past work in agent based-models of ungulate foraging (Morales et al., 2005). Stopover sites provide foraging and resting habitat, which are important to migratory ungulates as they allow animals to maximize energy intake by migrating in concert with plant phenology (Sawyer and Kauffman, 2011). This study incorporates limiting factors in vegetation availability due to both seasonality and disturbances (not addressed in Turner et al., 1994).

This research incorporates understandings from past work in the impacts of semi-permeable barriers of development, in which animals maintain connectivity to their seasonal ranges yet encounter disturbances (Sawyer et al., 2013). Development has the potential to encourage detouring, increase movement rates, and reduce the area of stopover use by individuals (Sawyer et al., 2013).

4.b. Emergence

The emergent properties of the model are the fitness of the herd population, the number of occurrences when the herd becomes ‘stressed’, variations in the distance traveled, and the frequency of the presence of the deer population on each 200 m parcel in the landscape. These properties emerge from changes in expansion of urban and energy development.

4.c. Adaptation

Based on its threshold to forage, each deer will either migrate or stop to forage. If they need to stop to forage, but the vegetation is insufficient, they will continue to migrate even when fitness is low. Deer can only forage on certain types of vegetation (see Table 2); if not located in a cell with such vegetation present, deer will continue to migrate to another cell to seek food while simultaneously expending energy.

4.d. Objectives

The objective of the deer is to maintain their fitness above the threshold to forage, and depending on the time of year, to migrate to their home ranges. This fulfills their migratory goals and increases their chances of accessing sufficient and quality vegetation.

4.e. Sensing

Each deer evaluates its immediate environment within its assigned search radius when foraging and migrating. Deer sense the type of vegetation present, the amount of vegetation they can consume, and their own energy level in comparison to the foraging threshold.

4.f. Interaction

Deer interact indirectly through foraging dynamics. As each deer forages, it both gains energy as well as depletes the amount of vegetation available within the cell. During the winter, when all deer are grouped together in a shared winter range, vegetation is depleted at an increased rate. As each deer forages in this small area, it decreases the amount of vegetation available for the other deer.

4.g. Stochasticity

Each deer is randomly assigned preferred summer and winter ranges that fall within seasonal home ranges and the 10km buffer of observed GPS-collar locations. Deer are also assigned a randomized initial fitness (between 0 and 100) at the initialization of the model. When migrating, the search radius distance is randomly selected from the random normal distribution defined by the range of observed distances traveled by GPS collared deer.

4.h. Collectives

Deer do not act as members of groups or interact with other individuals in the model. However, these fifty-three deer are meant to represent a simplification of sub-herd dynamics, and represent larger collectives that exist in the real world. This assumption is supported by GPS collar studies in which collared individuals are assumed to represent the larger herd group (Sawyer et al., 2009).

4.i. Observation

When a deer is migrating, every segment traveled is tracked to retain a count of how far that deer traveled during the simulation. Each deer's fitness is also tracked. These reporters are totaled for each time step and for each deer. An additional observation output included a tracking of the number of times each 200m² parcel was visited by a deer. The extent to which development (urban and energy) builds out from existing development is set and recorded in the initialization of the model. Each deer makes decisions on 2-hour intervals, however output data are collected every 10 days, a decision made to decrease the processing time of the model runs.

5. Initialization

At $t=0$ there are fifty-three deer present in the landscape, and each deer is located in their preferred summer range and has a preferred winter range. Deer fitness is a randomly selected value between 0 and 100, and development is set based on an expansion radius for urban development and minimum distance placement for energy development.

6. Input data

See section 2.b. for a full description of input data and attribute specifics.

7. Submodels

7.a. Fitness

Fitness (D_E) for each deer is randomly selected between 0 and 100. This fitness value is conceptual and allows for calibration of the model. A level of 100 is considered optimal, and if fitness falls below 0, the deer is considered ‘stressed’. The fitness threshold (F_T) in which deer need to forage ranges between 20 and 80, and if fitness falls below this threshold deer will want to forage. If fitness is above the threshold deer will continue to migrate. During the fall migration (S_f), one of two seasonal migrations (S), the deer loses fitness at a rate of 5.6 per 200 m traveled (d), and during the spring migration (S_s) loses energy at a rate of 3.8 per 200 m traveled (d). The deer will stop and forage if fitness falls below the threshold to forage. For each 2-hour period the deer forages at a 200 m patch of land, fitness increases by 5.6 in the fall and 3.8 in the spring.

If $S = S_f$ and $D_E < F_T$:

$$D_E = D_E(t-1) - d(5.6)$$

If $S = S_s$ and $D_E < F_T$:

$$D_E = D_E(t-1) - d(3.8)$$

The observed data indicate that deer spend more time stopped foraging in the spring, and less time stopping to forage in the fall. These values were calculated from analyzing only migratory segments of the GPS collar data, and calculating the time each deer spent in a 200 m location (presumably foraging). During the spring deer spent more time foraging (hence the 3.8 value to calibrate more time spent at stopovers to increase fitness), and during the fall migration deer spent less time foraging (hence the 5.6 value to calibrate less time spent in stopovers to increase fitness). Ungulate energetics rules for this study were developed as a simplified version from Turner et al. (1994). Maintenance, or the energy spent for basic life purposes (i.e. maintaining body heat, digesting food, etc.), was not included. For each 2-hour period that the deer is foraging, the 200 m patch where it stands is depleted by the same value that the deer is taking in (i.e. 5.6 in the fall and winter and 3.8 in the spring and summer). If there is increased development in the landscape, there is less available vegetation in the landscape for foraging, and a higher probability that deer will have to select a developed plot of land. This is particularly critical when deer are in their winter range, where the majority of urban and energy development is present.

7.b. Foraging

Foraging and fitness principles were derived from past agent based-models of ungulate foraging (Morales et al., 2005). The model begins at the start of fall migration, when vegetation quality and availability is less than during the spring and summer (Short et al., 1966). Vegetation that has potential for deer to forage (see Table 3) is given an initial food-value of 50 during the fall and winter, and during the spring and summer this

value is reset to 100, a method of calibration to represent two general stages of forage availability and quality, and provide a means to calibrate the energy consumption of deer and forage availability during the fall/winter and spring/summer.

Table 3: Vegetation type and deer forage potential.

Landcover type (NLCD 2011)	Percentage of time spent (based upon GPS locations)	Deer forage potential? (Nicholson et al. 1997)
Shrub/scrub	75.0%	Yes
Evergreen forest	14.7%	Yes
Herbaceous	4.4%	Yes
Deciduous forest	2.4%	Yes
Woody wetlands	1.4%	Yes
Emergent herbaceous wetlands	0.1%	Yes
Hay/pasture	0.1%	Yes
Developed, open space	< 0.1%	No
Mixed forest	< 0.1%	Yes
Barren land	< 0.1%	No
Developed, low intensity	< 0.1%	No
Open water	< 0.1%	No
Developed, medium intensity	< 0.1%	No
Cultivated crops	< 0.1%	No
Perennial snow/ice	0%	No
Developed, high intensity	0%	No

7.c. Migration

The deer assesses its fitness and continues to migrate towards its home range if fitness is above the threshold to forage. If migrating, each deer chooses a distance to migrate based on a random normal distribution, which defines the search radius in which the deer can select a patch with a preferred landcover type based on its observed preferences. The random normal distribution of distance traveled was calculated between time points of 2-

hours, and as it was a skewed distribution, a log transformation was applied to the data. A normal distribution with a mean of 4.85 and a standard deviation of 1.2 was determined to be the best fit for the range of distance traveled, and the cone of vision of the deer within the selected search distance was calibrated at 180°.

7.d. Development

Urban development expands from existing development at a radius of 0 m (low development) to 2,000 m (high development), and energy development is dispersed at minimum distances from other energy development features, ranging from 200 m apart (high development) to 2,000 m apart (low development) (see Figure 3).

ArcGIS was utilized for initial data analysis and processing (ESRI), and the agent-based model was developed in NetLogo (NetLogo).

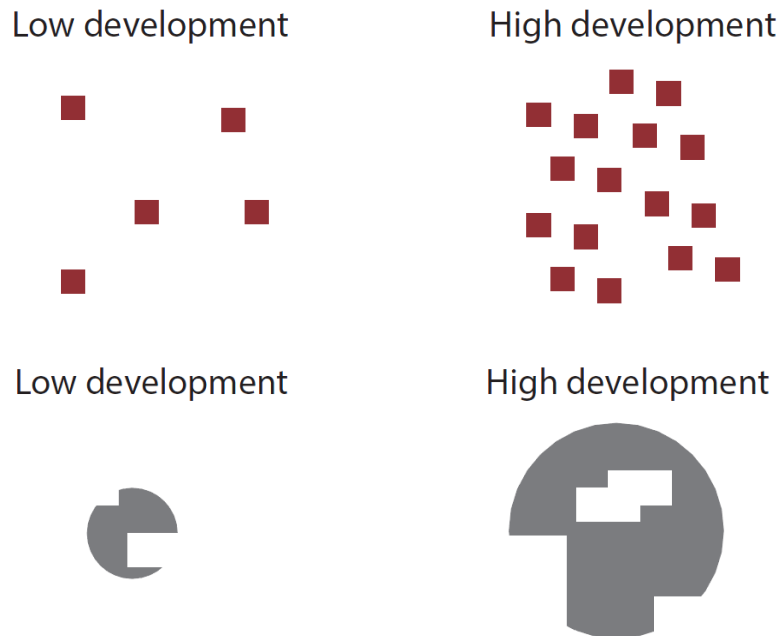


Figure 3: Comparisons of low and high development spatial arrangements for both energy and urban development.

CHAPTER III

RESULTS

Model Calibration

Data were collected based on 10-day intervals in order to run the analysis within an appropriate time frame (approximately 40 hours for all results and runs). Each parameter configuration was repeated a total of 30 times, a repetition value that was also selected in order to run the analysis within the appropriate time frame.

The model was calibrated by performing a sensitivity test to determine the appropriate threshold to forage that most closely mirrored patterns in fitness observed in the real world. The threshold to forage was examined at stages of 20, 40, 60, and 80 (see Figure 4). Mule deer fitness tends to be low during the winter (due to lower availability of quality vegetation) and high in the summer (more abundant quality vegetation) (Mautz, 1978). These thresholds were tested in environments with no additional urban or energy development to examine the threshold at the ‘current’ environmental state. When the threshold to forage is set at a value of 60 or 80 there is no fluctuation between seasons, an unrealistic scenario. For thresholds set at 20 and 40 there is an apparent trend in lower fitness during the winter and higher fitness during the summer. At a threshold to forage of 40 the overall fitness of the population ranges between 2,900 to 3,600 in the winter and 3,400 to 4,100 in the summer.

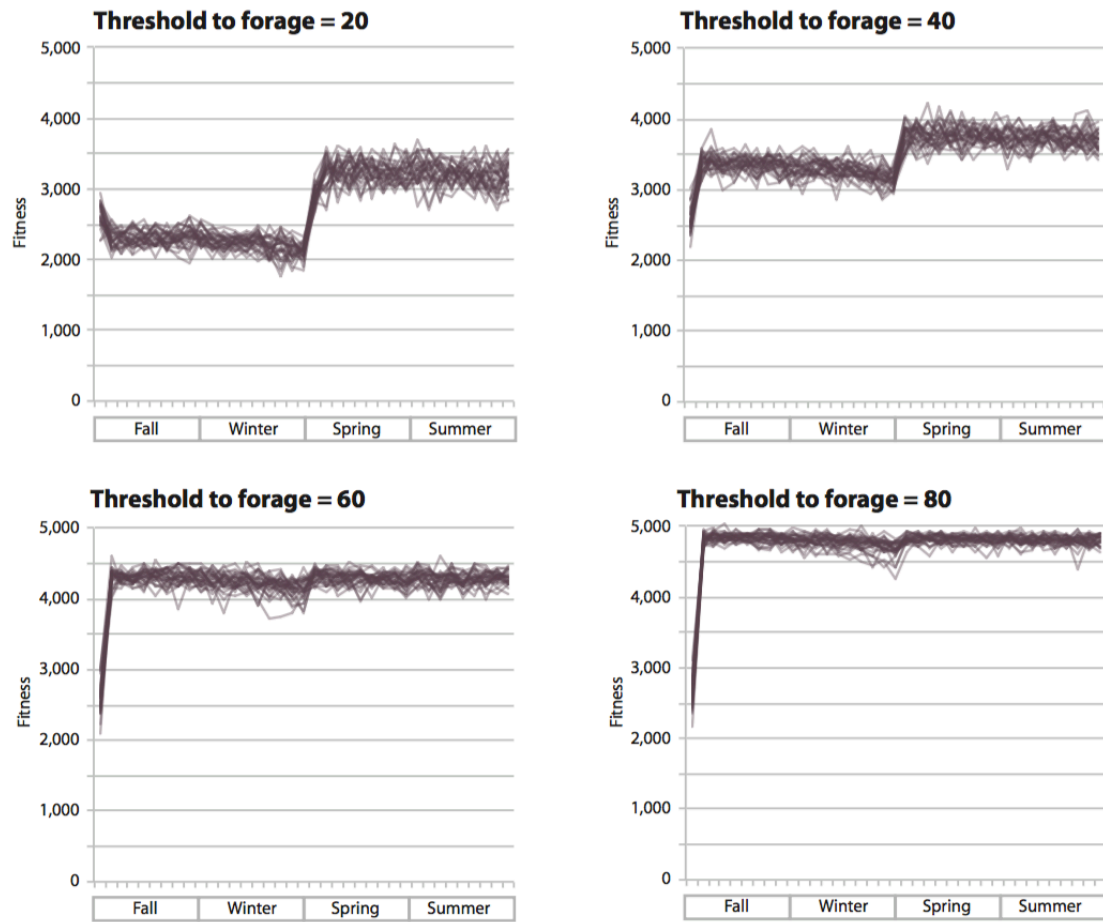


Figure 4: Variations in the forage threshold.

Impacts of Urban Development

Deer fitness in response to changes in urban development was examined at expansion radius intervals of 0 m, 400 m, 800 m, 1,200 m, 1,600 m, and 2,000 m. A radius of 0 m represents urban development in its current (i.e. 2011) state, and a radius of 2,000 m represents the highest extent of urban development, considered a high-development stage. The threshold to forage remained constant at 40 based on calibration results, and energy development remained constant at a minimum distance of 2,000 m, which is the low energy development scenario in which energy development features are spread furthest apart. Figure 5 illustrates the average fitness for all fifty-three deer during the different scenarios of urban development. When urban development is expanded at radiuses of 400 m, 800 m, and 1,200 m fitness levels do not fluctuate. When urban development is expanded to radiuses of 1,600 m and greater overall deer fitness declines below 3000 (an average fitness of 56 for each individual) during the late winter.

Stress events are events when an individual's fitness falls below 0. For urban development scenarios with expansion radiuses of 400 m and 800 m, the total number of stress events at the end of the year remained below 750, and for urban development scenarios with expansion radiuses of 0 m, 1,200 m, 1,600 m, and 2,000 m the total number of stress events at the end of the year increases to around 1000 events. Figure 6 demonstrates the gradual increase in the number of stress events as the year progresses.

As urban development increases, the number of stress events that occur during particular seasons of the year varies for different urban development scenarios. Figure 7 demonstrates the difference in stress events between each ten-day interval in the model. During the fall the frequency of stress events remains below or close to 100 for each ten-

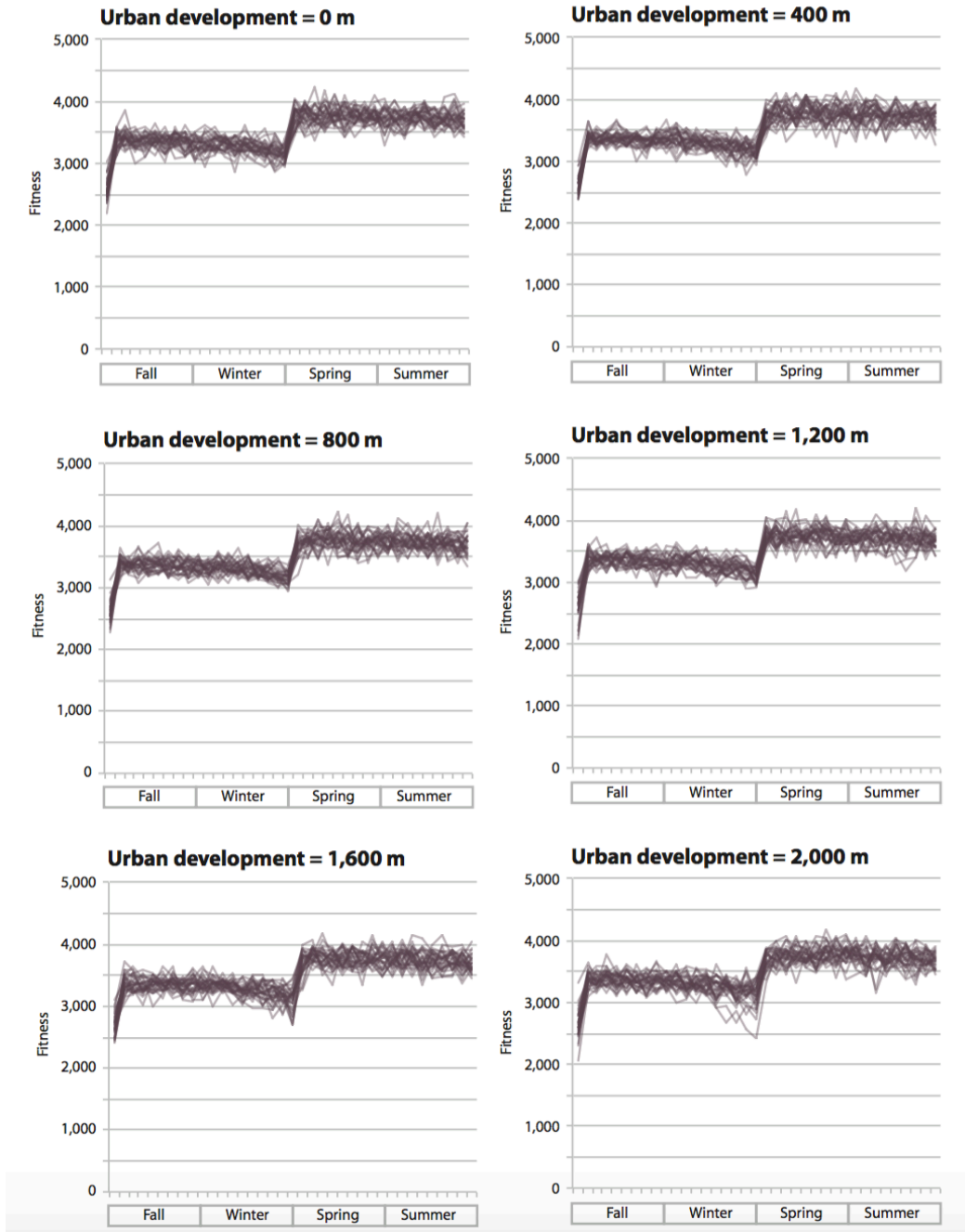


Figure 5: Effects of urban development on overall fitness. The threshold to forage remains constant at 40, and energy development remains constant at a minimum distance of 2,000 m. Urban development is expanded to radiuses of 0 m (low development), 400 m, 800 m, 1,200 m, 1,600 m, and 2,000 m (high development).

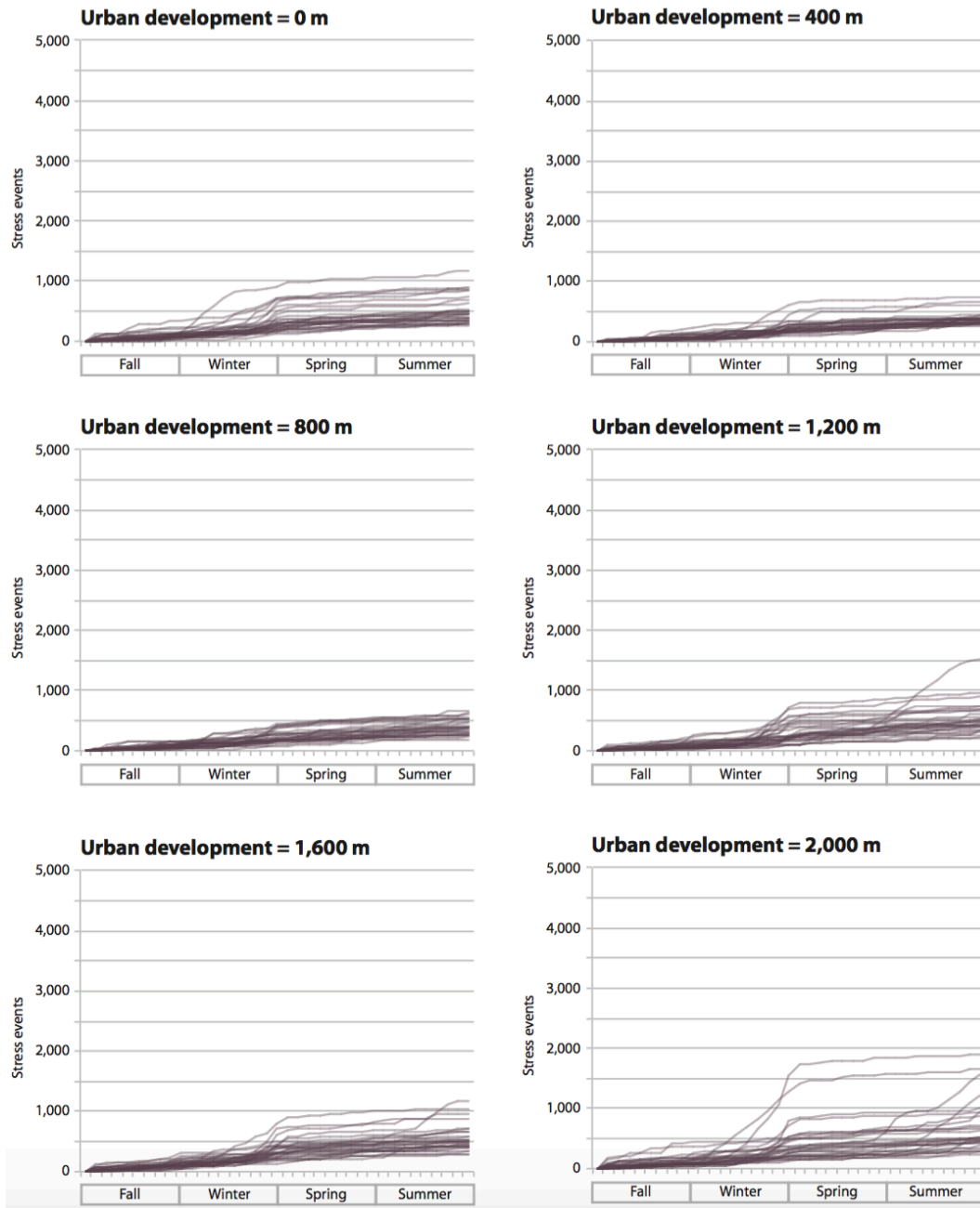


Figure 6: Effects of urban development on cumulative number of stress-events. The threshold to forage remains constant at 40, and energy development remains constant at a minimum distance of 2,000 m. Urban development is expanded to radiuses of 0 m (low development), 400 m, 800 m, 1,200 m, 1,600 m, and 2,000 m (high development).

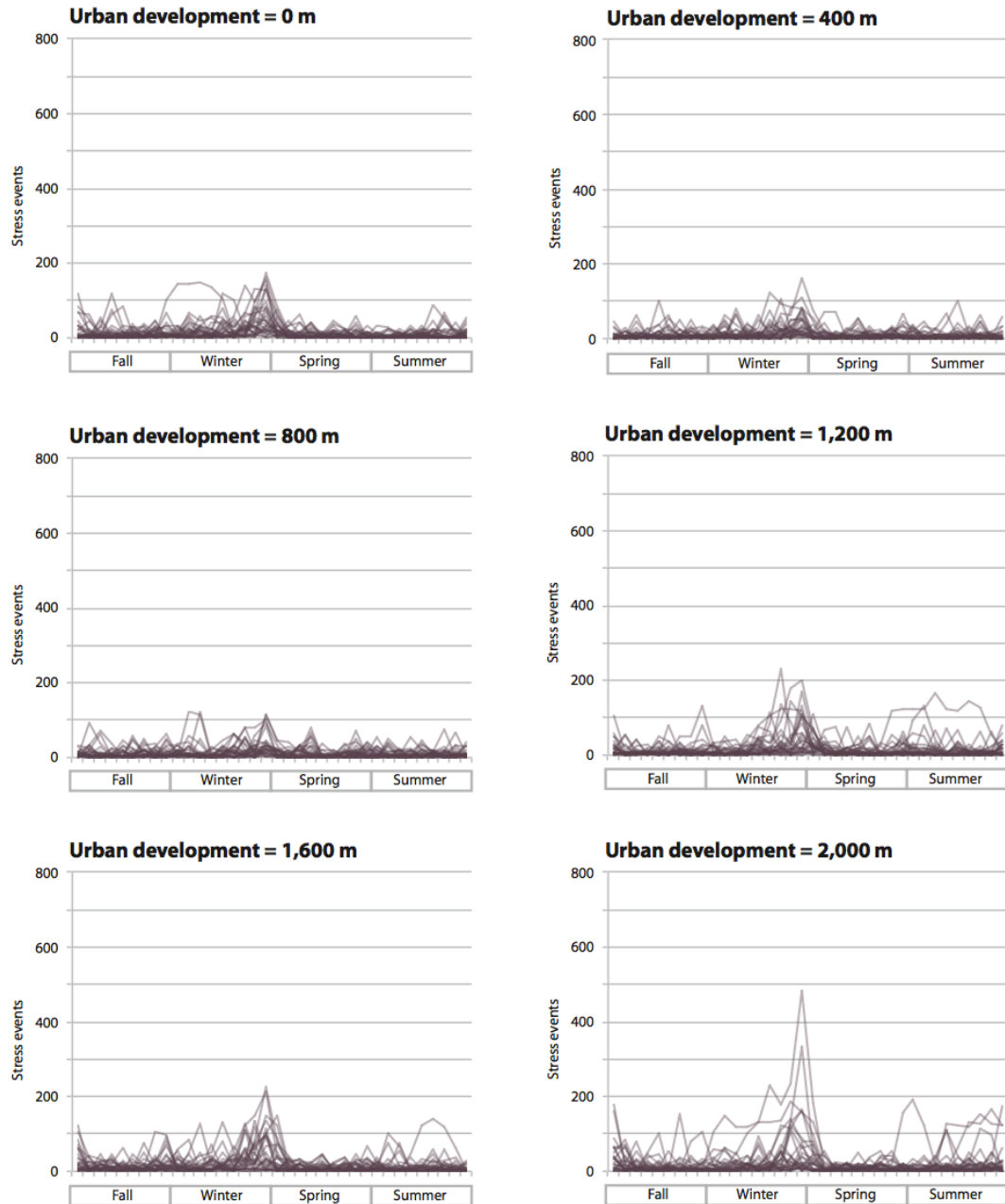


Figure 7: Effects of urban development on frequency of stress-events. The threshold to forage remains constant at 40, and energy development remains constant at a minimum distance of 2,000 m. Urban development is expanded to radiuses of 0 m (low development), 400 m, 800 m, 1,200 m, 1,600 m, and 2,000 m (high development).

day period for all scenarios of urban development. When urban development is expanded to a radius of 800 m, the number of stress events in each ten-day interval remains around 100. When development is reduced to 0 m (2011 development scenario) and 400 m the number of stress events during the winter increases to 175 for each ten-day interval, and when development is expanded to 1,200 m and 1,600 m the number of stress events per ten-day interval increases to 200 in the winter, with increases in stress events during late spring and early summer to 100 stress events. In the highest urban development scenario of 2,000 m, stress events increase to 500 in the winter and 200 in the late spring and summer.

Impacts of Energy Development

Changes to deer fitness in response to changes in energy development were examined for six different levels of development. Development was measured based off of the minimum distance between energy development features in the landscape. Development scenarios examined minimum distances of 200 m, 400 m, 800 m, 1,200 m, 1,600 m, and 2,000 m. A minimum distance of 200 m represents the highest energy development scenario, and a minimum distance of 2,000 m represents the lowest development scenario. The threshold to forage remained constant at 40 based on calibration results, and urban development remained constant at a expansion radius of 0 m, the lowest urban development scenario. Figure 8 illustrates the average fitness for all fifty-three deer during the different energy development scenarios. When minimum distances are set at 2,000 m, 1,600 m, 1,200 m, 800 m, and 400 m fitness follows the same patterns of decline in the winter and incline in the summer, with only a few runs in which the overall

fitness of the population declines more severely during the winter, falling below 3000. However, in the high development scenario, where energy features are placed 200 m apart, almost all model runs exhibit winter fitness that dips below 3000 to around 2500.

For the energy development scenarios with a minimum distance of 200 m the total number of stress events at the end of the year rise to above 1500 and, in some runs, reach totals of 3000 to 5000. For energy development scenarios with minimum distances of 2,000 m and 1,200 m, the total number of stress events are consistently below 1500, and the same is true for minimum distances of 1,600 m, 800 m, and 400 m, aside from one to two runs during which the total number of stress events for the year was at 1700. Figure 9 demonstrates the gradual increase in the number of stress events as the year progresses.

The number of stress events that occur during particular seasons of the year varies for different energy development scenarios. Figure 10 demonstrates the difference in stress events between each ten-day period for all scenarios of energy development. In the high energy development scenario, stress events occur 200 times for each ten-day period in the fall and summer, and increase to significantly to 800 stress events during the winter. When energy development is decreased to a minimum distance of 400 m, the increase in stress events for ten-day intervals begins in the late fall, rising to 350 during the winter. In the summer, stress events increase to 100. When the minimum distance for energy development is at 800 m, winter stress events during ten-day intervals increase to 200, but also increase in the summer to over 100 stress events, and at 1,200 m winter stress events increase to 300. When energy development minimum distances are set at 2,000 m and 1,600 m, the number of stress events that occur in ten-day intervals during the fall, spring, and summer remain below 100, and in the winter increases to 200 stress events.

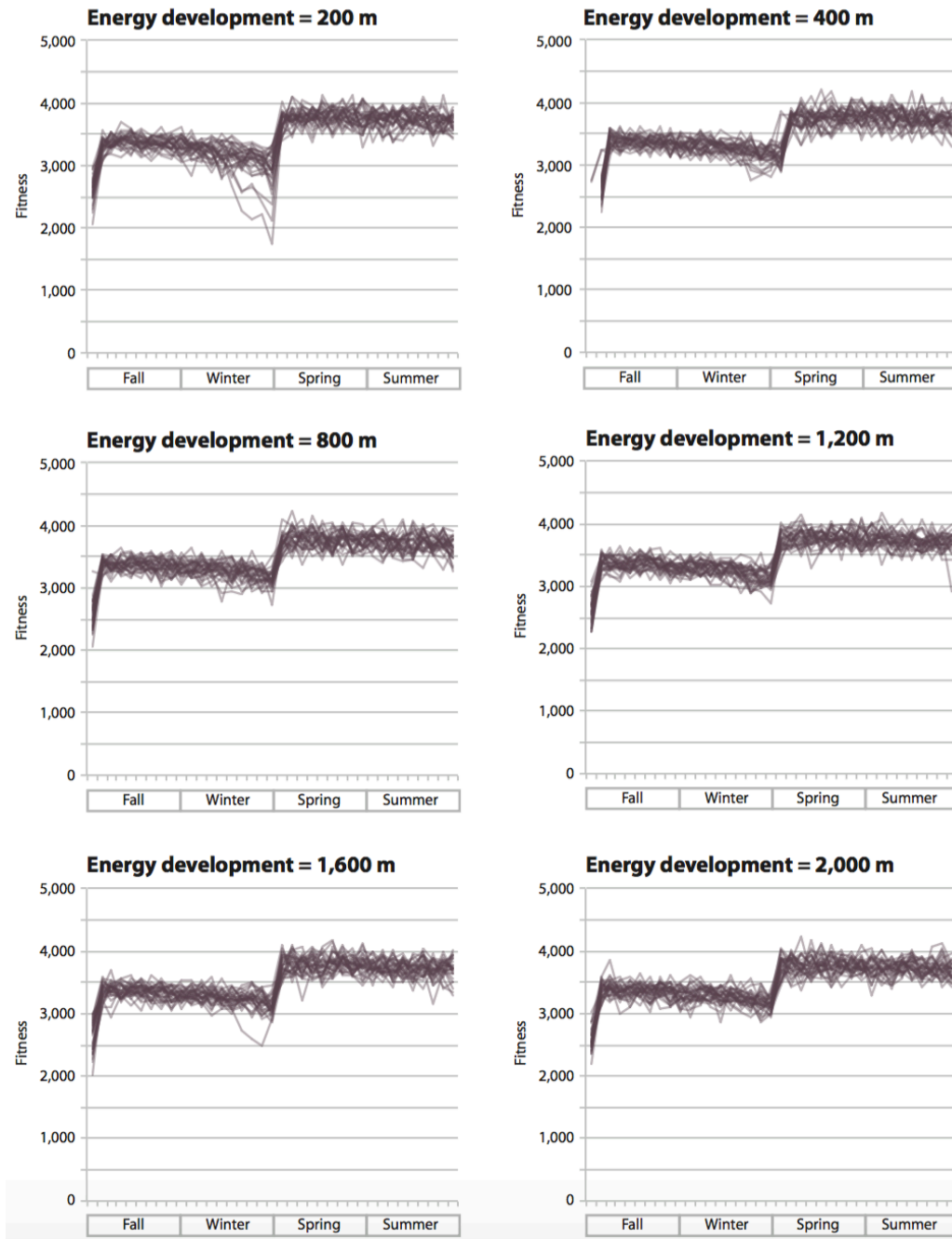


Figure 8: Effects of energy development on overall fitness. The threshold to forage remains constant at 40, and urban development remains constant at an expansion radius of 0 m. Energy development is placed at minimum distances of 200 m (high development), 400 m, 800 m, 1,200 m, 1,600 m, and 2,000 m (low development).

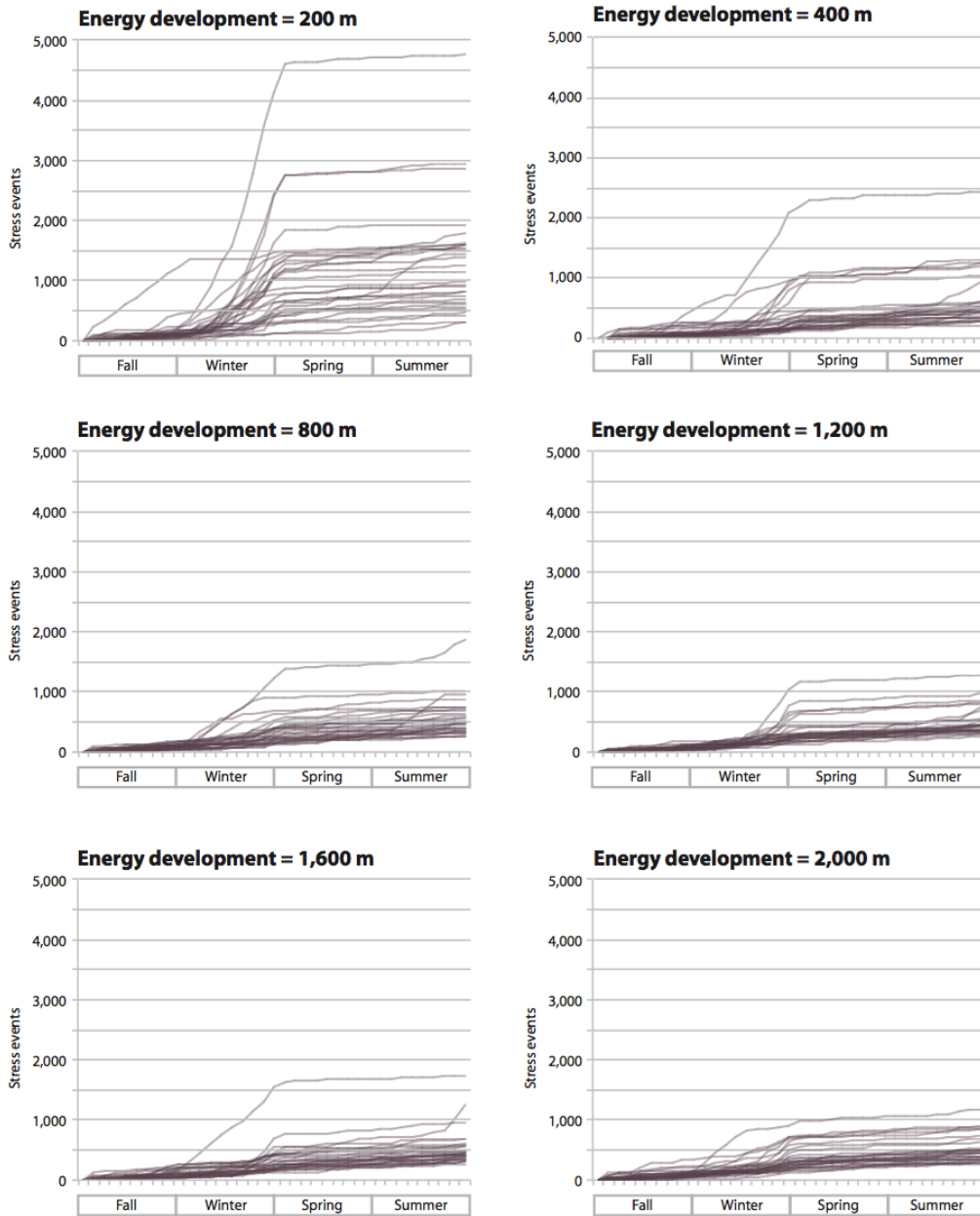


Figure 9: Effects of energy development on cumulative number of stress-events. The threshold to forage remains constant at 40, and urban development remains constant at an expansion radius of 0 m. Energy development is placed at minimum distances of 200 m (high development), 400 m, 800 m, 1,200 m, 1,600 m, and 2,000 m (low development).

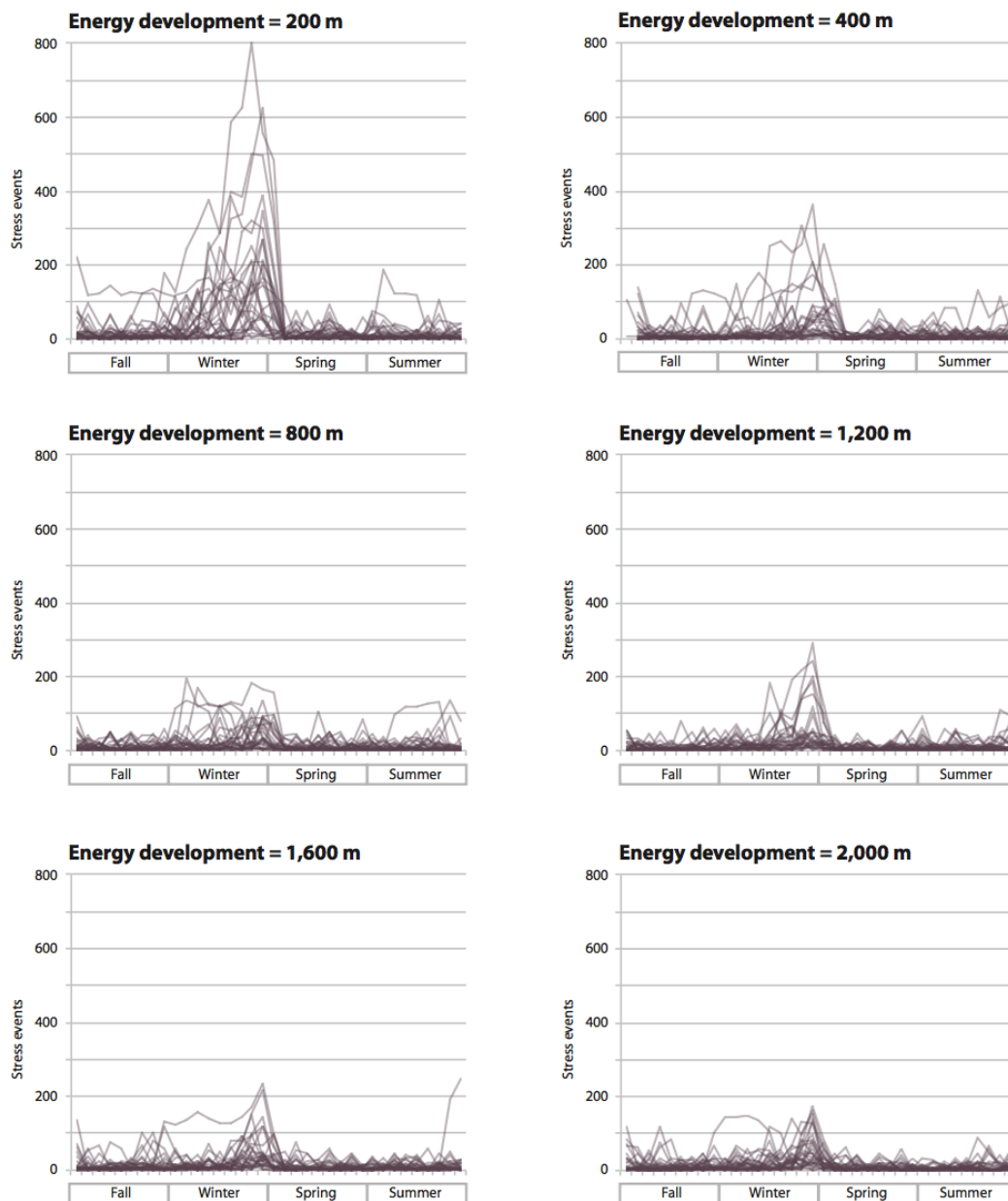


Figure 10: Effects of energy development on frequency of stress-events. This figure shows the number of stress events, divided into 10-day intervals, for each of the six energy development scenarios. Energy development is placed at minimum distances of 200 m (high development), 400 m, 800 m, 1,200 m, 1,600 m, and 2,000 m (low development).

Impacts of Urban and Energy Development in High Development Scenarios

When urban and energy development are both increased to high development scenarios (expansion radius of 2,000 m for urban development and minimum distance of 200 m for energy development) deer have a significantly higher frequency of stress events (Figure 11), and deer are increasingly stressed during seasons other than winter. Deer are most stressed in the winter, with the frequency of stress-events every ten-days in the fall and late summer increased compared to other development scenarios.

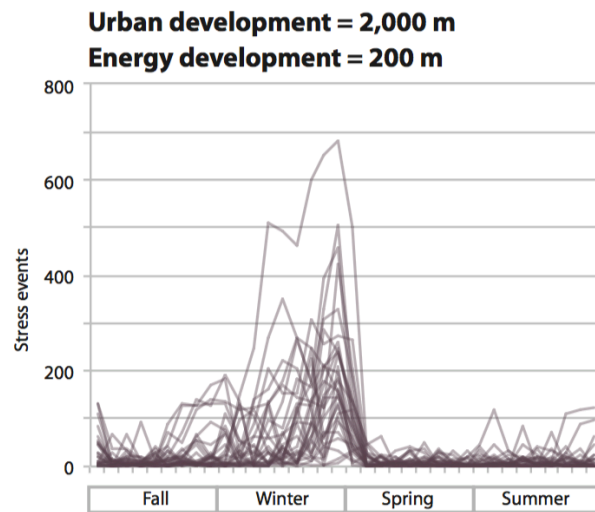


Figure 11: Effects of high energy and urban development on frequency of stress events. This figure shows the number of stress events, divided into 10-day intervals, for high energy (minimum distance of 200 m) and high urban development (expansion radius of 2,000 m).

CHAPTER IV

DISCUSSION

Previous research in the fields of wildlife biology, animal migration, and ecology has examined the dynamics of migratory ungulates and potential for human impact, however there has been limited research that incorporates modeling and mapping techniques that examine multiple barriers to migration at a population-level scale (Copeland et al., 2009). The objective of this research is to use a complex systems modeling approach to evaluate: *how do the spatial arrangement and extent of urban and energy development impact migrating mule deer populations in Western Wyoming?* An agent-based model was developed to address the research objective, and this method incorporated multiple human stressors to examine how these stressors impact migratory mule deer. The modeling approach and results presented in this study provide a method for evaluating the impacts that expanding urban and energy development will have on mule deer, and this study also provides a platform from which to expand an agent-based model of migration to include other environmental factors that influence ungulate fitness. The study incorporated multiple environmental stressors to be assessed simultaneously, and provided a means for assessing how various development scenarios and spatial arrangements impact mule deer fitness.

The results from the model simulations suggest that urban development has a greater impact on mule deer in high development scenarios than low development scenarios, and is in agreement with research conducted by Polfus and Krausman (2012). However, it is unexpected that urban development would have a significantly lower impact on mule deer than energy development. Another key finding is that there is low variability in mule

deer responses to the various scenarios of urban development, indicating that it is probable that mule deer will frequently be impacted in similar ways in each urban development arrangement. Stress events were a greater indicator of impact than overall fitness of the herd, which is unexpected. This may be attributed to the frequency of data collection in model runs (every ten days), which misses fine scale declines in fitness during encounters with development, particularly during the winter.

Energy development has a greater impact on mule deer than urban development as measured by the frequency of stress events, and responses to energy development in the form of stress events also display a much higher level of variability among model runs. This variability indicates uncertainty in how deer respond to energy development in the landscape, as well as how they respond to different spatial arrangements of development features. By considering both multiple migrations and time spent in home ranges to examine impacts, this modeling approach provides new insight into how mule deer may respond to development activities, and fills gaps in which energy development has only been assessed at either a home range level or migratory route level (Dyer et al., 2002; Sawyer and Nielson, 2010; Thomson et al., 2006). As energy development is increased and is clustered more closely together, deer are impacted at earlier stages as compared to urban development. This does not reflect that urban development is less important than energy development, but that in combination with energy development deer reach stressed states more frequently.

This research expands existing knowledge by examining multiple future scenarios, and determining the level of expansion in which deer are most greatly impacted. The study also examined spatial patterns of development in the landscape, and how the spatial

arrangements of both urban and energy development impact mule deer fitness. Different activities that occur at urban and energy development sites (i.e. noise, traffic, etc.) were not incorporated into this model, highlighting that solely various land use change scenarios and spatial arrangements of development can have a significant impact on mule deer. Understanding of how activities on development sites impact wildlife has been addressed as key to understanding impacts of development to ungulates (Walker et al., 2007; Sawyer et al., 2009; Northrup and Wittemeyer, 2012), however the understanding of the spatial patterns and arrangements of development in the landscape are also critical to understanding how mule deer will be impacted by future development. Urban development may have less of an impact than energy development for two reasons: 1) energy development is concentrated in the shared winter range, where deer frequently encounter barriers (or ‘stressors’) when searching for quality forage when there is less available and 2) the spatial arrangement and expansion of urban development allow deer to go around barriers, versus the spatial arrangement of energy development, where the placement of features is more complex and allows for multiple results in impacts to mule deer, with an increased level of variability and uncertainty. Energy development has a varied, more complex spatial arrangement than urban development, and it is that pattern that is impacting mule deer in particular. This research has shown that different spatial patterns of development in the landscape lead to varied impact scenarios, and that the dispersal of development may be more important than activity for both urban and energy development.

The agent-based modeling and complex systems theory approaches applied in this study assessed how future landscape changes from both urban and energy development

together change fitness and migratory dynamics of mule deer, and allowed for the development of modeling and mapping techniques that examined multiple barriers to migration (Copeland et al., 2009). This complex systems theory approach to understanding the impacts of development on mule deer migration evaluates multiple stressors to mule deer, as well as examines impacts at a population-level. It also provides a basis for understanding the underlying processes that drive animal behavior and spatial decision-making (Tang and Bennett, 2010). Agent-based models have been utilized to study movement of other ungulates such as elk (Bennett and Tang, 2006), caribou (Semeniuk et al., 2012), and moose (Grosman et al., 2011), however this is the first complex systems approach to evaluate mule deer dynamics and potential impacts to their fitness. This model is simple yet complex, and provides a basis for exploring and developing mule deer decision-making rules and a platform for further understanding the impact of urban and energy development to wildlife. Rules and values for fitness are rudimentary, yet these simple rules and processes lead to large-scale patterns in how deer react to and are impacted by increased development in the environment. Additionally, further work needs to be done to examine how the selection of temporal resolution impacts model results. While it is preferred to have fine resolution, there are limits to conducting this computationally. However, with increased computational power this research could examine the model sensitivity to the selection of temporal resolution.

It is important to be mindful of what was excluded in this study. Ungulate reproduction was not accounted for (similar to Turner et al. (1994)), and direct individual interactions were also excluded. Reproduction and direct agent-to-agent interactions were excluded because the model was not representative of the entire herd population, and

there were no direct measures of reproduction. In a multi-year evaluation of the model, with a real-world herd population size (abundance), reproduction, and life-cycle dynamics (survival) should be included in the analysis. Climate and vegetation ‘green-up’ (phenology) were also excluded in order to develop a simplified base from which impacts of development to mule deer can be explored, but could be included in any expanded versions of this study. For development potential characteristics, surface and sub-surface land ownership were also excluded to maintain simplicity in the model.

Future research directions that would be beneficial to branch from this project include more detailed inputs for areas open to development. Rules for development should be specific to particular land ownership and managers, and should also incorporate multiple development planning scenarios and wildlife management needs. This provides an opportunity to uncover energy and urban development planning and policy strategies through a multi-objective decision making approach that addresses both mule deer population needs and development objectives. The multi-objective decision making approach has the capability to address complexity in geographical problems (Xiao et al., 2002) and generate optimal or near-optimal solutions to the problems addressed (Xiao et al., 2006). Future research should also incorporate indirect impacts of urban and energy development, i.e. noise, traffic, etc., and how these factors may influence mule deer behavior. Changes to habitat are more obvious and direct when vegetation is replaced by energy development or urban infrastructure.

CHAPTER V

CONCLUSION

Mule deer migration is a complex process that is susceptible to various types of human development in the landscape, including urban and energy development that have the potential to create barriers or reduce access to seasonal habitat requirements. Agent-based modeling and complex systems theory provide opportunities to examine how the spatial arrangement and extent of urban and energy development impact migratory mule deer populations in Western Wyoming. This approach can be expanded in the future to examine other migratory populations or identify optimal or near-optimal development strategies that can help mitigate impacts to mule deer. This research would benefit from the incorporation of climate and dynamic vegetation variables to examine additional components critical to mule deer.

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